

***Craterellus atrobrunneolus* sp. nov. from southwestern China**

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ABSTRACT—A new ectomycorrhizal fungus from southwestern China, *Craterellus atrobrunneolus*, is proposed as supported by morphological and phylogenetic analyses. The basidiocarps are characterized by a dark brown to brownish gray coloration, convex to plano-convex pileus with an umbilicate but not perforate center, smooth to slightly folded gray to cretaceous hymenophore, absence of clamp connections in all tissues, narrow basidia with 2–6 sterigmata, and broadly ellipsoid to subglobose basidiospores. Maximum likelihood and Bayesian sequence analyses of the ITS + nrLSU DNA regions confirm the phylogenetic position of the new species. Illustrations accompany the technical description and comparisons of *C. atrobrunneolus* and closely related species.

KEY WORDS—*Cantharellales*, *Hydnaceae*, taxonomy

Introduction

Craterellus Pers. is typified by the species *C. cornucopioides* (L.) Pers. (Persoon 1825). The genus, characterized by funnel-shaped fruiting bodies with a hollow stipe that may also be highly reduced (Petersen 1979), is closely related to *Cantharellus* Adans. ex Fr. from which it is distinguished mainly by the absence of clamp connections (Corner 1957, 1966; Bigelow 1978). However, some species that lack clamp connections have been also included

in *Cantharellus* (Yomyart & al. 2012; Wilson & al. 2012; Buyck & al. 2014; Bijesh & al. 2018). *Craterellus* was previously classified in *Cantharellaceae* (*Cantharellales*) (Wilson & al. 2012; Henkel & al. 2014), but Hibbett & al. (2014) now indicate that *Cantharellaceae*, *Hydnaceae*, *Clavulinaceae*, and *Sistotremataceae* are synonymous, and *Hydnaceae* has priority as the correct name of the combined family. As ectomycorrhizal fungi, *Craterellus* species are symbiotic with canopy trees of the genera like *Aldina*, *Castanopsis*, *Cedrus*, *Cyclobalanopsis*, *Dicymbe*, *Hopea*, *Pakaraimaea*, *Pinus*, *Quercus*, and *Schima* (Matheny & al. 2010, Smith & al. 2011, Kumari & al. 2012, Wilson & al. 2012, Buyck & al. 2014, Henkel & al. 2014, Kour & al. 2015, Bijesh & al. 2018, Zhong & al. 2018).

A total of 154 names have been recorded in this genus, and 76 species are currently accepted (<http://www.indexfungorum.org>). Most species are edible and often colorful (Zhong & al. 2018), although ten or so species are dark gray, dark brown, or black in color (Persoon 1825; Peck 1878; Burt 1914; Smith 1968; Petersen 1969, 1975; Wilson & al. 2012; Yomyart & al. 2012; Bijesh & al. 2018). Most *Craterellus* species have been described from South America (Wilson & al. 2012, Henkel & al. 2014) and North America (Dahlman & al. 2000, Dunham & al. 2003, Porter & al. 2008, Wright & al. 2009, Matheny & al. 2010, Raja & al. 2017) plus several from Europe (Dahlman & al. 2000, Harrington & Mitchell 2002, Tibuhwa & al. 2012, Osmundson & al. 2013) and about ten species from Asia (Masse 1906, Bresadola 1913, Corner 1966, Kumari & al. 2012, Hembrom & al. 2017, Das & al. 2017, Bijesh & al. 2018, Zhong & al. 2018). Only two species (*C. aureus* Berk. & M.A. Curtis and *C. luteus* T.H. Li & X.R. Zhong) have been originally described from China (Zhong & al. 2018).

During the investigation on macrofungi in southwestern China, a dark *Craterellus* species was collected from an angiosperm forest in Shizong County, Yunnan Province. We describe it as a new species, based on morphological characters and molecular analyses.

Materials & methods

Morphological studies

Specimens are deposited at the herbarium of Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, China (IFP). Microscopic procedures followed Lu & al. (2018). Microscopic drawings were made with the aid of a drawing tube. Microscopic studies used sections mounted in Cotton Blue (CB): 0.1 mg aniline blue dissolved in 60 g pure lactic acid; CB+/- = cyanophilous/acyanophilous. Amyloid and dextrinoid reactions were tested in Melzer's reagent (IKI): 1.5 g KI (potassium

TABLE 1. *Craterellus* species, specimens, and sequences used in the phylogenetic analyses, with a *Hydnum ellipsosporum* outgroup.
Type materials are annotated with [T].

SPECIES	ITS	nrLSU	VOUCHER	LOCALITY
<i>C. albostrigosus</i>	–	MG593194	CAL 1624 [T]	India
<i>C. atratoides</i>	JQ915093	JQ915119	MCA1313	Guyana
	JQ915103	JQ915129	TH8473	Guyana
	JQ915111	NG042660	TH9232 [T]	Guyana
<i>C. atratus</i>	JQ915092	JQ915118	MCA1070	Guyana
	JQ915100	JQ915126	MCA990	Guyana
	JQ915107	JQ915133	TH9203	Guyana
<i>C. atrobrunneolus</i>	MN902353	MN894058	IFP 019359 [T]	China
<i>C. caeruleofuscus</i>	MH558300	MH558300	TENN 073179	USA
<i>C. cinereofimbriatus</i>	JQ915104	JQ915130	TH8999	Guyana
	JQ915105	JQ915131	TH9075 [T]	Guyana
	JQ915112	JQ915138	TH9264	Guyana
<i>C. cornucopioides</i>	–	AF105298	UPSF-11800	USA
	–	AF105299	UPSF-11801	USA
	–	AF105301	HbO-53302	Norway
<i>C. excelsus</i>	JQ915102	JQ915128	TH8235 [T]	Guyana
<i>C. ignicolor</i>	–	AF105314	UPSF-11794	USA
<i>C. indicus</i>	NR119831	NG060387	PUN 3884 [T]	India
<i>C. inusitatus</i>	–	MG593195	CAL 1625 [T]	India
<i>C. luteus</i>	MG727896	MG701171	GDGM48105 [T]	China
	MG727897	MG727898	GDGM46432	China
<i>C. lutescens</i>	–	AF105302	UPSF-11789	Sweden
	–	AF105303	UPSF-11790	Sweden
	–	AF105304	UPSF-11791	Spain
<i>C. odoratus</i>	–	AF105306	UPSF-11799	USA
<i>C. olivaceoluteus</i>	JQ915098	JQ915124	MCA3186	Guyana
	JQ915109	JQ915135	TH9205 [T]	Guyana
<i>C. parvogriseus</i>	MF421099	MF421098	CAL 1533 [T]	India
<i>C. pleurotoides</i>	JQ915097	JQ915123	MCA3124	Guyana
	JQ915110	JQ915136	TH9220	Guyana
	KT339208	KT339208	TH8877	Guyana
<i>C. shoreae</i>	–	KY290585	CAL 1396 [T]	India
<i>Craterellus</i> sp.	–	KM484695	BB 09.079	India
	JQ915091	JQ915117	AWW263	Malaysia
	KJ786699	KJ786611	G3211	Guyana
	KJ786682	KJ786577	G2070	Guyana
<i>C. strigosus</i>	JQ915094	JQ915120	MCA1750	Guyana
	JQ915108	JQ915134	TH9204 [T]	Guyana
<i>C. tubaeformis</i>	EU057081	EU057081	ECUBC19	Canada
	KP454008	KP454008	UBC F28404	Canada
	DQ474413	–	SWUBC511	Canada
Uncult. ECM	AB251810	–	Pdmt4	Japan
<i>Hydnum ellipsosporum</i>	KX086215	KX086217	FD3281	Switzerland

iodide), 0.5 g I (crystalline iodine), 22 g chloral hydrate, aq. dest. 20 ml; IKI- = neither amyloid nor dextrinoid reaction. 5% KOH was used as a mountant. Sections were studied at magnifications up to $\times 1000$ using a Nikon Eclipse E600 microscope with phase contrast illumination; dimensions were estimated subjectively with an accuracy of 0.1 μm . Surfaces of the basidiospores and basidia were observed with a Phenom Prox scanning electron microscope (ESEM) at an accelerating voltage of 10 kV. For spore measurements, the apiculus was excluded. In presenting the spore size ranges, 5 % of the measurements at each end of the range are given in parentheses. The following abbreviations are used in the text: L = mean spore length; W = mean spore width; Q = variation in the ratios of L/W between specimens studied; n = number of spores measured from a given number of specimens. Terminology for descriptive terms follows Vellinga (1988) and special color terms are from Kornerup & Wanscher (1978).

Molecular procedures and phylogenetic analyses

Phire Plant Direct PCR Kit procedures were used to extract total genomic DNA from the basidiocarps. Polymerase chain reactions (PCR) were performed on a Bio-Rad T100TM Thermal cycler. The DNA was amplified in a 30 μl reaction mixture comprising 0.9 μl template DNA, 15 μl of 2 $\times$ Phire Plant PCR buffer, 1.5 μl of each primer, 0.6 μl Phire HS II DNA Polymerase, and 10.5 μl ddH₂O (double distilled water). The nuc rDNA ITS1-5.8S-ITS2 region (ITS) was amplified with the primers ITS1-F (5'CTTGGTCATTTAGAGGAAGTAA3') and ITS4 (5'TCCTCCGCTTATTGATATGC3') (White & al. 1990). The 28S nuclear rDNA region was amplified with the primers LROR (5'ACCCGCTGAACCTTAAGC3') and LR5 (5'TTAAAAAGCTCGTAGTTGAAC3') (Vilgalys & Hester 1990). The PCR thermal cycling program condition was set as follows: initial denaturation at 95 °C for 5 min; followed by 35 cycles at 95 °C for 30 s, either 57.2 °C (for ITS1-F/ITS4) or 52 °C (for LROR/LR5) for 30 s and 72 °C for 30 s; and a final extension at 72 °C for 7 min. PCR amplification was confirmed on 1% agarose electrophoresis gels stained with ethidium bromide. DNA sequencing was performed at the Beijing Genomics Institute (BGI), and the newly generated sequences were submitted to GenBank.

The sequences were processed in GenBank (<http://www.ncbi.nlm.gov>) using the BLAST option and downloaded (TABLE 1). The ITS and nrLSU dataset includes the new species and other closely related species. Sequences were aligned using Clustal X (Thompson & al. 1997). Maximum likelihood (ML) analysis was performed in RAxML v8.2.4 with GTR + I + G model (Stamatakis 2014). Bayesian analysis with MrBayes 3.2.4 (Ronquist & Huelsenbeck 2003) implementing the Markov Chain Monte Carlo (MCMC) technique and parameters predetermined with MrModelTest2.3 (Posada & Crandall 1998; Nylander 2004) were performed and the parameters in MrBayes were set as follows: lset nst = 6, rates = invgamma. Four simultaneous Markov chains were run starting from random trees and keeping one tree every 100th generation until the average standard deviation of split frequencies was <0.01. The value of burn-in was set to discard 25% of trees when calculating the

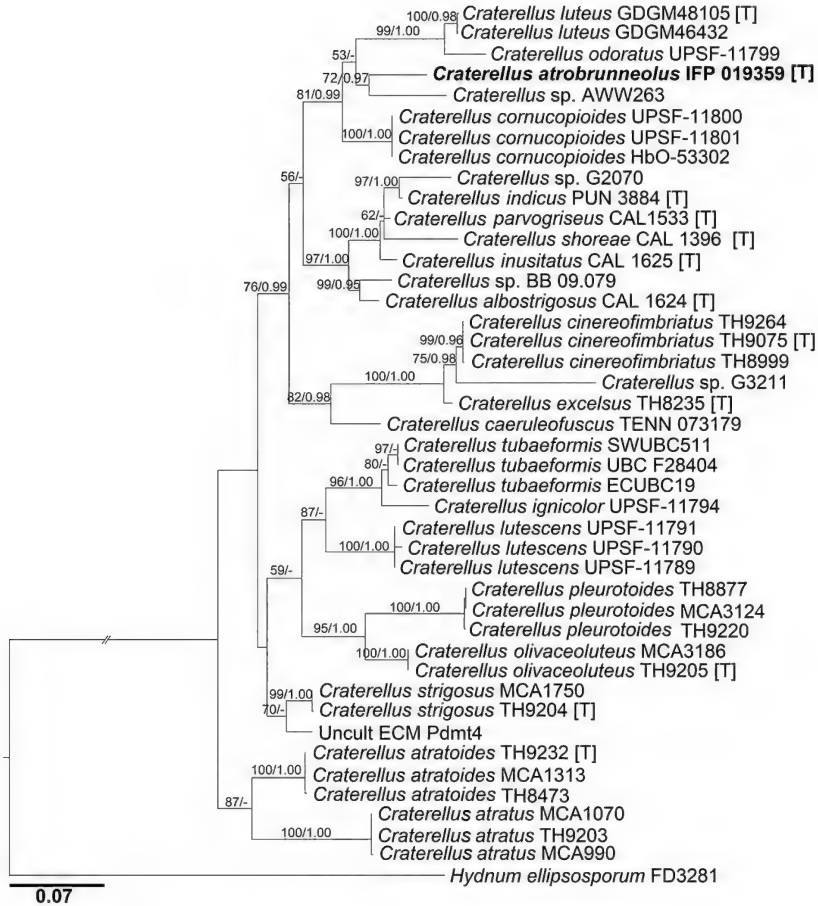


FIGURE 1. Maximum likelihood tree illustrating the phylogeny of *Craterellus atrobrunneolus* and related taxa based on ITS + nrLSU sequences dataset. The type materials are annotated with [T]. Branches are labeled with maximum likelihood bootstrap support >50% and Bayesian posterior probabilities >0.95.

posterior probabilities. Bayesian posterior probabilities were obtained from the 50% majority rule consensus of the trees kept.

Phylogenetic results

The ITS + nrLSU dataset included 43 sequenced specimens, representing our new species, 24 other identified or putative *Craterellus* species, and the outgroup

Hydnum ellipsosporum Ostrow & Beenken. Bayesian analysis ran 2,000,000 generations and produced an average standard deviation of split frequencies = 0.006070. A similar topology (FIG. 1) was generated when the same dataset and alignment were analyzed using ML. In the phylogenetic tree, our new holotype specimen was closely related to an unidentified *Craterellus* species (AWW263) with moderate support and joined with the clade comprising *Craterellus luteus* and *C. odoratus* (Schwein.) Fr. with moderate support.

Taxonomy

Craterellus atrobrunneolus T. Cao & H.S. Yuan, sp. nov.

FIGS 2–4

MB 833932

Differs from *Craterellus strigosus* by its larger basidiocarps, smaller basidiospores, and absence of clamp connections on hyphae in all tissues.

TYPE: China. Yunnan Province, Shizong County, Junzishan Mt., on the ground in angiosperm forest, 8 Aug 2019, Yuan 13878 (Holotype, IFP 019359; GenBank MN894058, MN902353).

ETYMOLOGY: *atrobrunneolus*, referring to the dark brown to brownish gray basidiocarps.

BASIDIOCARPS annual, solitary to conrescent, soft and leathery when fresh, becoming friable and light in weight upon drying. **PILEUS** thin, 1.5–3.0 cm in diam, when young infundibuliform, in age becoming convex to plano-convex with a shallow depression at center, umbilicate (not perforate). **PILEAL SURFACE** dark brown (6F7/7F6/8F6) to almost black when moist, drying become brownish gray (6E3/6E2), subglabrous, regularly wrinkled to sparsely veined. **PILEAL MARGIN** slightly incurved, wavy, irregularly folded, crenate or sometimes incised. **HYMENOPHORE** bluish grey (23B2), smooth to slightly folded and down to the stipe. **PILEAL CONTEXT** very thin, grayish (1E1), leathery. **STIPE** confluent with pileus, 2.5–5.0 cm long and 0.3–1.5 cm diam, leathery or fleshy when fresh, soft corky upon drying, concolorous with the pileal surface; hollow, irregularly pitted, usually curved and eccentric; smooth to finely rugulose, not thickening substantially, 0.1–0.3 mm thick in section; stipe base somewhat bulbous. Odor mild; taste not distinctive.

BASIDIOSPORES broadly ellipsoid to subglobose, yellowish in 5% KOH, with granular contents; wall 0.5 μm thick; apiculus 0.5–1.0 μm long; CB+, IKI–, (6.2–)6.5–7.8(–8.0) $\times$ (4.2–)4.5–6.0(–6.2) μm , $L_m = 7.38 \mu\text{m}$, $W_m = 5.47 \mu\text{m}$, $Q = 1.35\text{--}1.52$ ($n = 60/2$). **BASIDIA** 45.5–70 $\times$ 5.2–8.5 μm long, narrow, subcylindric, subclavate to clavate, with large guttules or finely granulose contents, hyaline to yellowish in 5% KOH; 2–6 sterigmata, 3.5–6.0 μm long. **BASIDIOLES** 40.5–65 $\times$ 5.0–8.0 μm , abundant, cylindrical to subclavate,



FIGURE 2. *Craterellus atrobrunneolus* (holotype, IFP 019359). Basidiocarps.

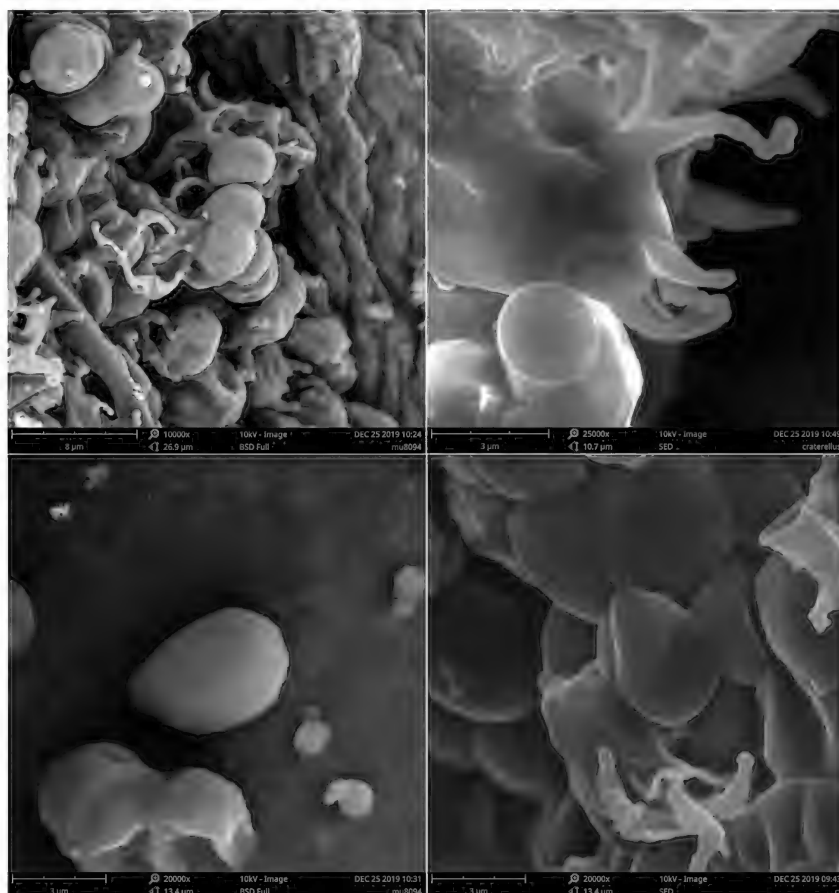


FIGURE 3. *Craterellus atrobrunneolus* (holotype, IFP 019359).
Basidia and basidiospores (SEM).

multiguttulate. CYSTIDIA absent. HYMENIUM 60–85 μm thick. HYMENOPHORAL TRAMA hyphae 3.5–10 μm diam., thin to slightly thick-walled, more or less interwoven, occasionally branched, often with fine guttules, hyaline to yellowish brown in 5% KOH. PILEAL TRAMA hyphae 5.5–10 μm diam., thick-walled, subregular. PILEIPELLIS composed of cylindrical hyphae, 3.5–11 μm diam, thick-walled, frequently branched, somewhat interwoven, with rounded obtuse apex. STIPITIPELLIS composed of interwoven hyphae, 3.5–7.5 μm diam., thick-walled; terminal elements 11.5–29 $\times$ 3.5–12 μm . Clamp connections absent in all tissues.

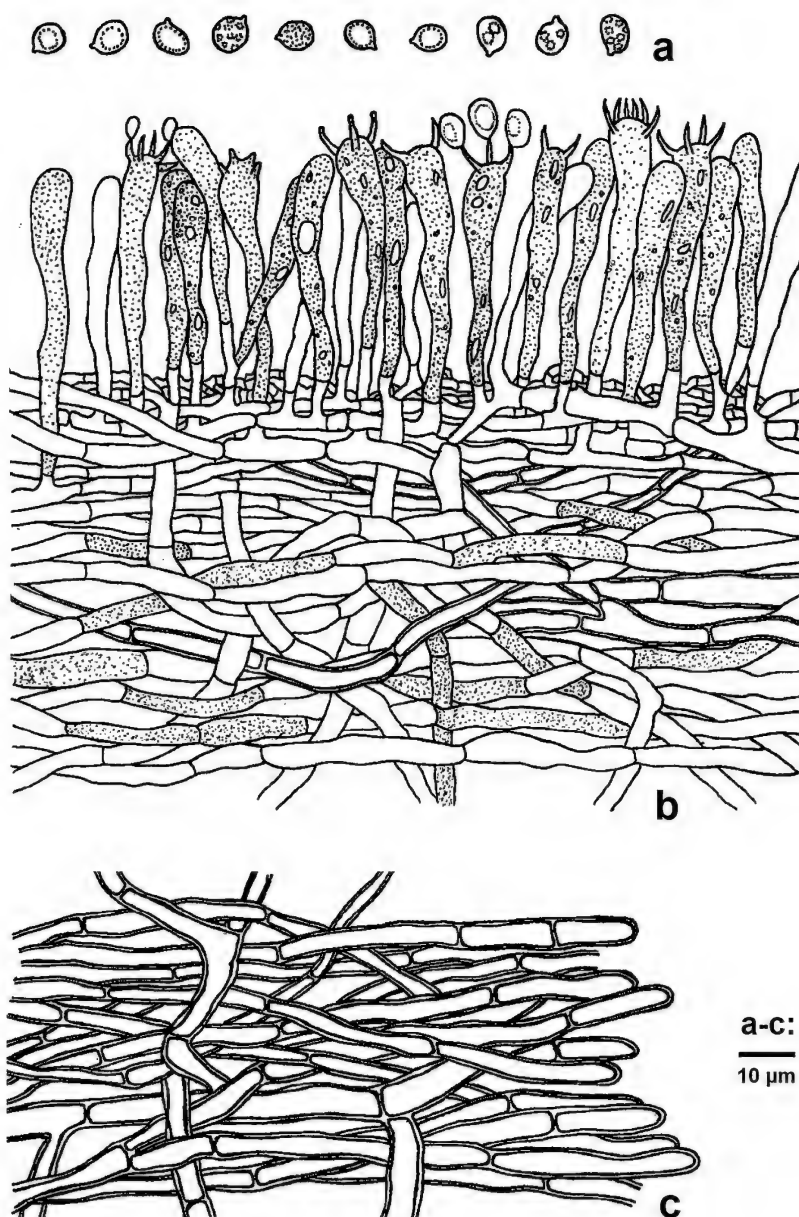


FIGURE 4. *Craterellus atrobrunneolus* (ex holotype, IFP 019359).
 a. Basidiospores; b. A section of context and hymenium; c. Pileipellis.

ADDITIONAL SPECIMEN EXAMINED— CHINA. YUNNAN PROVINCE, Shizong County, Junzishan Mt., ground in angiosperm forest, 8 Aug 2019, Yuan 13900b (IFP 019360).

Discussion

Craterellus atrobrunneolus is characterized by dark brown to brownish gray basidiocarps, convex to plano-convex pileus with an umbilicate (non-perforated) center, smooth to slightly folded gray to cretaceous hymenophore, narrow basidia with 2–6 sterigmata, and broadly ellipsoid to subglobose basidiospores.

Several *Craterellus* species also have similarly dark colored basidiocarps, such as *C. albostrigosus* C.K. Pradeep & K.B. Vrinda, *C. atratoides* T.W. Henkel & al., *C. atratus* (Corner) Yomyart & al., *C. caeruleofuscus* A.H. Sm., *C. cornucopioides* (L.) Pers., *C. fallax* A.H. Sm., and *C. strigosus* T.W. Henkel & al.

Craterellus albostrigosus, described from India, resembles the new species in its brownish pileus, gray hymenophore, thick-walled pileipellis hyphae, stipitipellis hyphae with short terminal elements, and absence of clamp connections. But *C. albostrigosus* is distinguished by its smaller (3–19 mm diam) pileus with white strigose hairs, a solid stipe with strigose scales, and larger ($9\text{--}11.5 \times 6\text{--}8 \mu\text{m}$) basidiospores (Bijeesh & al. 2018).

Craterellus atratoides resembles *C. atrobrunneolus* in its grayish brown glabrous pileus and stipe, gray hymenophore, densely guttulate basidioles, and ellipsoid to subglobose basidiospores but is distinguished by its broader ($7.1\text{--}9 \mu\text{m}$ diam) basidiospores, larger ($79\text{--}111 \times 7.4\text{--}9.9 \mu\text{m}$) basidia with 3–5 sterigmata, and abundant clamp connections (Wilson & al. 2012).

Craterellus atratus also shares similarly colored basidiocarps, ellipsoid basidiospores, a smooth to very faintly wrinkled hymenophore, and the absence of cystidia but is separated from *C. atrobrunneolus* by its smaller, campanulate basidiocarps (pileus 8–9 mm, stipe $7\text{--}9 \times 0.75\text{--}1 \text{ mm}$), solid stipe, larger ($9 \times 6\text{--}7 \mu\text{m}$) basidiospores, and rare clamp connections (Yomyart & al. 2012).

Craterellus strigosus, described originally from Guyana, resembles *C. atrobrunneolus* in its similarly shaped pileus, gray hymenophore, and multiguttulate basidia but is distinguished by its smaller basidiocarps (4–18 mm broad, 2–9 mm tall), wider ($5.9\text{--}8 \mu\text{m}$ diam.) basidiospores, stipe with dense, brown strigose scales, and abundant clamp connections in all tissues (Wilson & al. 2012).

The phylogenetic tree supports *Craterellus atrobrunneolus* as distantly related to *C. odoratus* and *C. luteus*, two species obviously separated from the

new species by their bright orange to greenish yellow pileal surface (Dahlman & al. 2000; Zhong & al. 2018).

Acknowledgments

We thank Jun-Fen Liang (Chinese Academy of Forestry, Guangzhou) and Xiao-Dan Yu (Shenyang Agricultural University, China) for presubmission review. This research was financed by the Biodiversity Investigation, Observation and Assessment Program (2019-2023) of Ministry of Ecology and Environment of China and the National Natural Science Foundation of China (Project Nos. 31770028 & 31970017).

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